Genetic variability

Clones within a coral reef

from Jared M. Diamond

A LARGE coral reef typically consists of many species, thousands of colonies and millions of polyps. But most corals can reproduce asexually, suggesting that many colonies are genetically identical members of the same clone. How many different genotypes are actually represented among the colonies of one coral species on a reef? A recent attack on this question by Cynthia Hunter[1,2] opens the way to studying the population genetics of one of the most important groups of marine organisms and will improve our understanding not only of corals but also of many other species of clonal animals.

Exploring the consequences of clonality requires methods for distinguishing members of the same and different clones. Most studies of these questions involve terrestrial plants[3-5]: recent histocompatibility studies of graft acceptance or rejection allow identification of putative clones among species of corals[6-9] or sponges[10-12]. A potential objection to these interpretations is that, whereas almost every individual vertebrate has a unique histocompatibility type, this might not be true of species in which histocompatibility depends on just a few loci. That fear has been realized: electrophoresis sometimes detects differences between individual corals sharing the same histocompatibility type[9,12-14]. The same objection can be raised against any method of clone identification that samples just a fraction of the genome. Comparing entire genomes is impractical, but the genome should at least be sampled in multiple ways.

Hunter worked with one of the most abundant coral species on Hawaiian reefs, *Porites compressa*, which reproduces sexually once a year by releasing eggs and sperm and may reproduce asexually at any time by colony fragmentation. A host of important conclusions about coral genetic composition, reproduction, age and evolution emerges from her analysis. The area under study included 291 *P. compressa* colonies and millions of polyps, most of which prove to belong to one of only eight genotypes, 40 per cent of them to one of only three genotypes. No colony is smaller than 60 cm^2, implying that successful larval settlement is rare and that asexual reproduction is far more frequent than sexual reproduction. From measured extents and growth rates of colonies, most colony ages were estimated at 4–21 years, but large colonies (greater than 10 m^2) may be hundreds or even thousands of years old[15,16]. Morphotypes differ in growth rates, competitive ability and distribution between leeward and windward sides of the reef.

Hunter selected a 2 × 10 m reef area off the Hawaiian island of Oahu and used four methods for identifying putative clones. First, she identified eight morphotypes on the *P. compressa* reef by differences in colour, length and width of branches and by distance between branch tips. That colonies can be visually distinguished by means of morphological characters is an important advantage of studying *P. compressa*.

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Finger-like colonies of the coral *Allopora nobilis* (courtesy of *Sagittarius*).

Second, she tested histocompatibility by grafting a branch of one colony to a branch of either the same colony, a different colony of the same morphotype, or a colony of a different morphotype. Acceptance or rejection of the graft became evident within a few weeks. All results proved to be transitive: if colony A fused with colonies B and C, colonies B and C also fused with each other. Grafts between colonies that Hunter had assigned to different morphotypes were always rejected, whereas 82 per cent of grafts of colonies assigned to the same morphotypes fused. (The rejected 18 per cent mostly involved two hard-to-distinguish morphotypes classified early in the project, while she was still learning to detect subtle differences between morphotypes.)

Third, Hunter studied seven enzymes by starch-gel electrophoresis. Two proved monomorphic and therefore useless for distinguishing clones, but five were polymorphic. Each morphotype proved electrophoretically distinct, whereas all colonies of a given morphotype were electrophoretically identical. Most of the 8 × 7/2 = 28 morphotype pairs could be distinguished by means of three or fewer electrophoretic loci, but two of the pairs were identical at four loci and could be distinguished only by the fifth. Hence, for *P. compressa*, unlike some other coral species, electrophoresis and histocompatibility recognize the same sets of clones.

Finally, Hunter used high-performance liquid chromatography to separate seven ultraviolet-absorbing compounds that were methanol-extracted from coral tissues. The eight morphotypes could all be distinguished by their characteristic ultraviolet signatures, and colonies of the same morphotype proved identical.

Thus, each morphotype is unique in its histocompatibility traits, 5-locus genotype and ultraviolet signature. Within Hunter's 20 m^2 transect, one morphotype was represented by only a single colony, but the other morphotypes were multiply represented (by up to 38, and an average of 19, colonies). During the two years of Hunter's study the dominant colonies increased in area, the rare ones retreated. Genetic variability may itself exhibit great local variation: it may be maximal on new substrates available for colonization by sexually produced propagules, and minimal on old stable reefs where colonies are established mainly by fragmentation[8].

To appreciate the significance of Hunter's work, reflect that virtually every individual of a species practicing exclusively sexual reproduction (such as most vertebrates) represents a unique genotype. But many plants and invertebrates, plus a few vertebrates, reproduce asexually as well as sexually. The fitness of a genotype then depends on all the asexually produced ramets constituting the clone. As summarized recently by Jackson[3], "clonal growth — the formation of more than one individual of identical genetic composition — is a fundamental ecological adaptation that has far-reaching consequences for the population biology, morphology, development and evolution of such organisms". □

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